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A Mammalian Petrosal from the Early Cretaceous of Mongolia: Implications for the Evolution of the Ear Region and Mammaliamorph Interrelationships*

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ABSTRACT

A mammalian petrosal from the Early Cretaceous Khoobur locality, Guchin Us Somon, Mongolia, is described and the major vessels and nerves associated with it are restored. A cladistic analysis of 44 characters of the petrosal and associated structures across 15 ingroup taxa, including all mammaliamorphs for which petrosal morphology is known, identified nine equally parsimonious trees. The consensus tree placed the Khoobur petrosal within Mammalia at a trichotomy with Triconodontidae and Prototribosphenida (*Vincelestes* + Theria). In the Khoobur fauna are gobiconodontids and symmetrodonts, which could account for such a systematic allocation. Previous hypotheses of mammaliamorph interrelationships are compared with the results of our analysis. A close relationship of monotremes with therians and a position of docodonts outside Mammaliaformes are not supported here.

INTRODUCTION

Since 1990, the Mongolian Academy of Sciences and the American Museum of Natural History have conducted paleontological research in Mesozoic and Cenozoic outcrops of Mongolia. In the summer of 1991, screenwashing at the locality of Khoobur (also var-

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iously spelled Khobur, Khoboor, and Khovboor), Guchin Us Somon, yielded a collection of small mammals. Included were isolated teeth, fragmentary upper and lower jaws, postcranial remains, and two petrosals, the more complete of which is reported here. Khoobur beds are believed to be of ?Aptian-Albian Age (Early Cretaceous) based on the known fauna (Clemens et al., 1979; Kielan-Jaworowska and Dashzeveg, 1989).

The petrosal is a topologically complex bone of the mammalian skull that is associated with a variety of soft-tissue structures, including the organs of hearing and balance, the central and peripheral nervous systems, major cranial arteries and veins, and muscles derived from the mandibular and hyoid arches (Goodrich, 1930; Novacek, 1993). Many of these soft tissues leave impressions on the petrosal in extant mammals and, therefore, can be reconstructed in fossil material (Wible, 1990; Rougier et al., 1992). Additionally, the impressions left by various soft tissues on the petrosal have proven to be of systematic value for determining higher-level phylogenetic relationships among mammals (Wible, 1986, 1987, 1990; Wible and Hopson, 1993).

Petrosals, and cranial remains in general, of Mesozoic mammals are rare. In fact, petrosals of Early Cretaceous age have been recovered for only two identifiable taxa: *Vincelestes* from the Hauterivian La Amarga Formation of Argentina (Bonaparte and Rougier, 1987) and partially described, unnamed triconodontids from the Aptian Cloverly Formation of Montana (Crompton and Jenkins, 1979). Another fragmentary petrosal of indeterminate mammalian affinities was reported from the Aptian-Albian Kelvin Formation of Utah by Prothero (1983). Discovery of a petrosal in the Khoobur beds thus affords another opportunity to investigate the anatomy of this bone in an Early Cretaceous mammal and to explore the evolution of this complex part of the skull in early mammals and their relatives.

MATERIALS AND METHODS

The Khoobur petrosal is cataloged as PSS-MAE-104 in the collections of the Geological Institute of the Mongolian Academy of Sciences, Ulaan Bataar, Mongolia.

The definition of taxonomic units employed here follows Gauthier (1986) and Rowe (1987). We use the terms Eucynodontia (Kemp, 1988; see comments by Hopson, 1991), Mammaliamorpha, Mammaliaformes, Mammalia, Theriimorpha, and Theria (Rowe, 1988), Holotheria (Hopson, 1994), Cladotheria and Tribosphenida (McKenna, 1975), Symmetrodonta (Prothero, 1981), and Prototribosphenida (Rougier, 1993). Gobiconodontidae and Triconodontidae are treated here as monophyletic taxa, even though relationships among "Triconodonta" are not fully resolved. At least in one instance (Rowe, 1993), *Gobiconodon* and *Triconodon* have been identified as sister taxa and we refer to this group informally as triconodonts.

To evaluate the affinities of the Khoobur petrosal, we scored the distribution of 44 characters across 15 ingroup taxa. We had the opportunity to study all the taxa included here, with the exception of *Megazostrodon.* Most of the characters employed were taken from the literature and corrected or supplemented according to our observations (see Appendix 1). The literature sources are: Kermack (1963), Kuhn (1971), Kermack et al. (1981), Sun (1984), Crompton and Sun (1985), Gow (1986), Kielan-Jaworowska et al. (1986), Novacek (1986), Sues (1986), Hahn (1988), Rowe (1988), Zeller (1989), Wible (1990, 1991), Lillegraven and Krusat (1991), Rougier et al. (1992), Crompton and Luo (1993), Lillegraven and Hahn (1993), Wible and Hopson (1993, 1995), Lucas and Luo (1993), Rougier (1993), Luo (1994), Luo and Crompton (1994), and Luo et al. (1995). To polarize characters, we chose as the outgroup the following non-mammalian eucynodonts: traversodontids, probainognathids, and chiniquodontids. The outgroup was polymorphic for five characters, which were scored as missing data. The resulting taxon-character matrix (see Appendix 2) was subjected to the branch and bound algorithm of PAUP (Swofford, 1993) and the **ie** command of Hennig86 (Farris, 1988). In both programs, all multistate characters were treated as unordered.

The scope of our analysis is limited by the available material, that is, an isolated petrosal. However, we do not believe that characters from this bone have more relevance

for the study of eucynodont phylogeny than do those from other anatomical systems.

The terminology for anatomical terms used here follows Wible (1987, 1990) and Rougier et al. (1992).

DESCRIPTIONS

The petrosal bone houses the organs of hearing and equilibration. It can be divided into two parts in extant mammals: the pars cochlearis, which is anteroventrally placed and includes the promontorium (the cochlear housing), and the pars canalicularis, which is posterodorsally placed and includes the semicircular canals. For descriptive purposes, we will describe the petrosal in four views—ventral, dorsal, lateral, and posterior—with the orientation based on the presumed position in the skull.

The specimen is a nearly complete, isolated right petrosal (figs. 1, 2). Articular surfaces are preserved for the exoccipital, supraoccipital, and squamosal bones. Missing is the anterodorsal part of the lateral flange, where the anterior lamina of the petrosal is expected. The ventral surface of the lateral flange is also broken in two places: a small break at its anteriormost end and a more extensive break posteriorly. On the promontorium, the anteriormost tip is missing. Where the articular surface of the basioccipital is predicted on the medial border of the petrosal, breakage exposes a deep channel. Small chips of bone are also missing from the tip of the paroccipital process, and there is slight erosion posterodorsal to the subarcuate fossa along the articular surface for the supraoccipital.

Ventral View (fig. 1A, B, C)

The pars cochlearis is represented by a narrow, elongate promontorium about 4 mm in length. Exposed at the broken anteriormost tip of the promontorium is a round, matrix-filled space. We are uncertain about the true nature of this space, but it might represent the rostral end of a straight cochlear duct, which is the shape predicted from the external morphology of the promontorium. Medial to the ventralmost prominence of the promontorium is a slightly concave surface that extends medially toward the presumed basioccipital suture. As stated above, the broken medial surface of the petrosal exposes a deep, smooth-walled channel, interpreted here as housing the inferior petrosal sinus. The posterior opening of this channel lies anteroventral to the jugular notch where a partially preserved foramen is visible. The anterior end of this channel curves laterally at the anterior pole of the promontorium (fig. 2) where it communicates with the lateral trough via a minute foramen.

On the posterolateral aspect of the promontorium is the elliptical fenestra vestibuli, which faces ventrolaterally and has its long axis oriented anteroposteriorly (fig. 1A, B). On the posterior aspect of the promontorium is the perilymphatic foramen. It is subequal in size to the fenestra vestibuli, nearly vertical in its orientation, and has a roughly quadrangular outline. Although a conspicuous groove for the perilymphatic duct is lacking, we identify this opening as a perilymphatic foramen because there is no certain cochlear aqueduct. A tiny foramen in the posterior part of the petrosal's contribution to the jugular foramen (not visible in fig. 1A) is too small and improperly positioned to be a cochlear aqueduct. It leads into the substance of the petrosal and probably transmitted a vein. The jugular foramen is similar in diameter to the perilymphatic foramen, as deduced from what is preserved on the petrosal. Separating the perilymphatic foramen from the fenestra vestibuli is a low, narrow bridge of bone, the crista interfenestralis, which gradually decreases in height posteriorly and does not reach the paroccipital process. The term crista interfenestralis has been used previously in sauropsids (Oelrich, 1956) for a structure that we interpret to be homologous with that in synapsids.

Running parallel to the promontorium is a deep, wide trough, the lateral trough. The deepest point of the lateral trough is located anteriorly where it is bounded medially by the nearly vertical lateral wall of the promontorium (figs. 1A, B, 2). Posterior to this striking depression are three foramina. The two more anteriorly placed foramina are interpreted as exits for branches of the facial nerve: the one in front for the palatine ramus and the other for the hyomandibular ramus (fig. 1C). The precise location of the aperture for the palatine ramus (the hiatus Fallopii)

cannot be determined because there is some bone missing along the preserved margin. However, we believe that the missing bone would only slightly increase the distance between the two preserved exits for the facial nerve branches. Posterolateral to the aperture for the hyomandibular ramus (the secondary facial foramen) is a slightly larger foramen (fig. 1A, B) that leads into a canal that opens endocranially on the dorsal surface (fig. 1D, E). This foramen is the tympanic aperture of the prootic canal, which in life transmitted the prootic vein.

The lateral extent of the lateral trough is bounded by a thickened crest of bone, the lateral flange (figs. 1A, B, 2). The preserved anterior portion of the lateral flange shows no contact facet for a quadrate ramus of the epipterygoid (alisphenoid). The preserved posterior portion is inflected medially to a

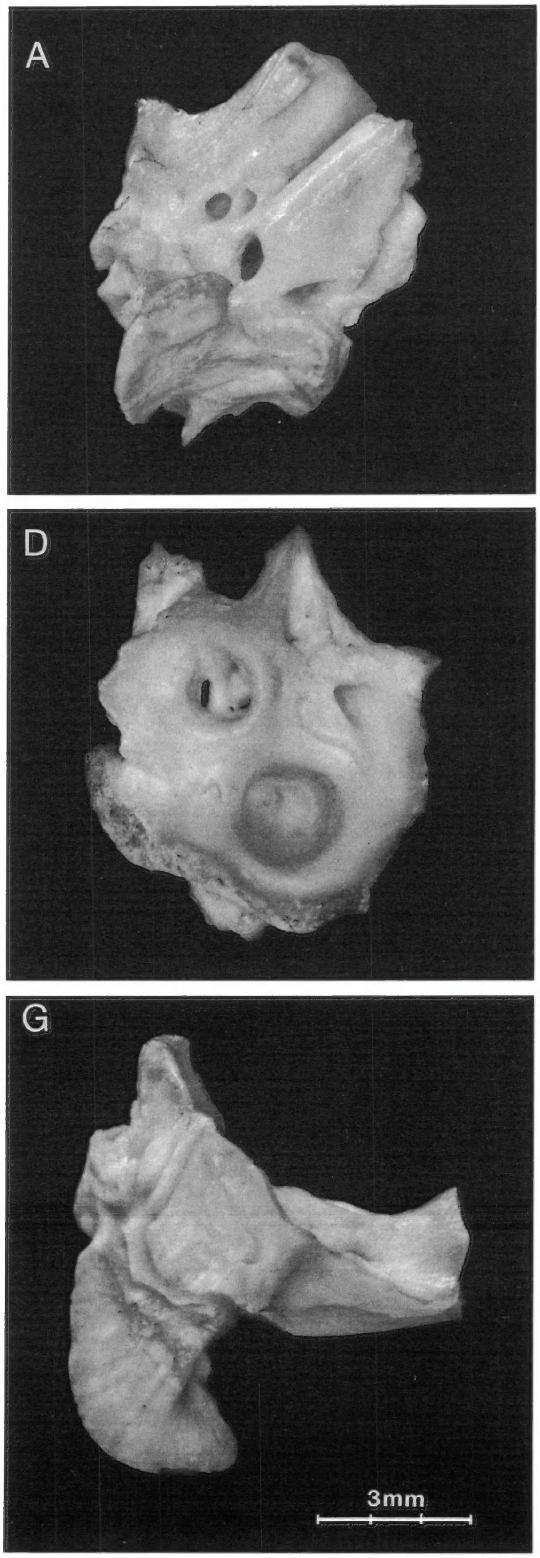
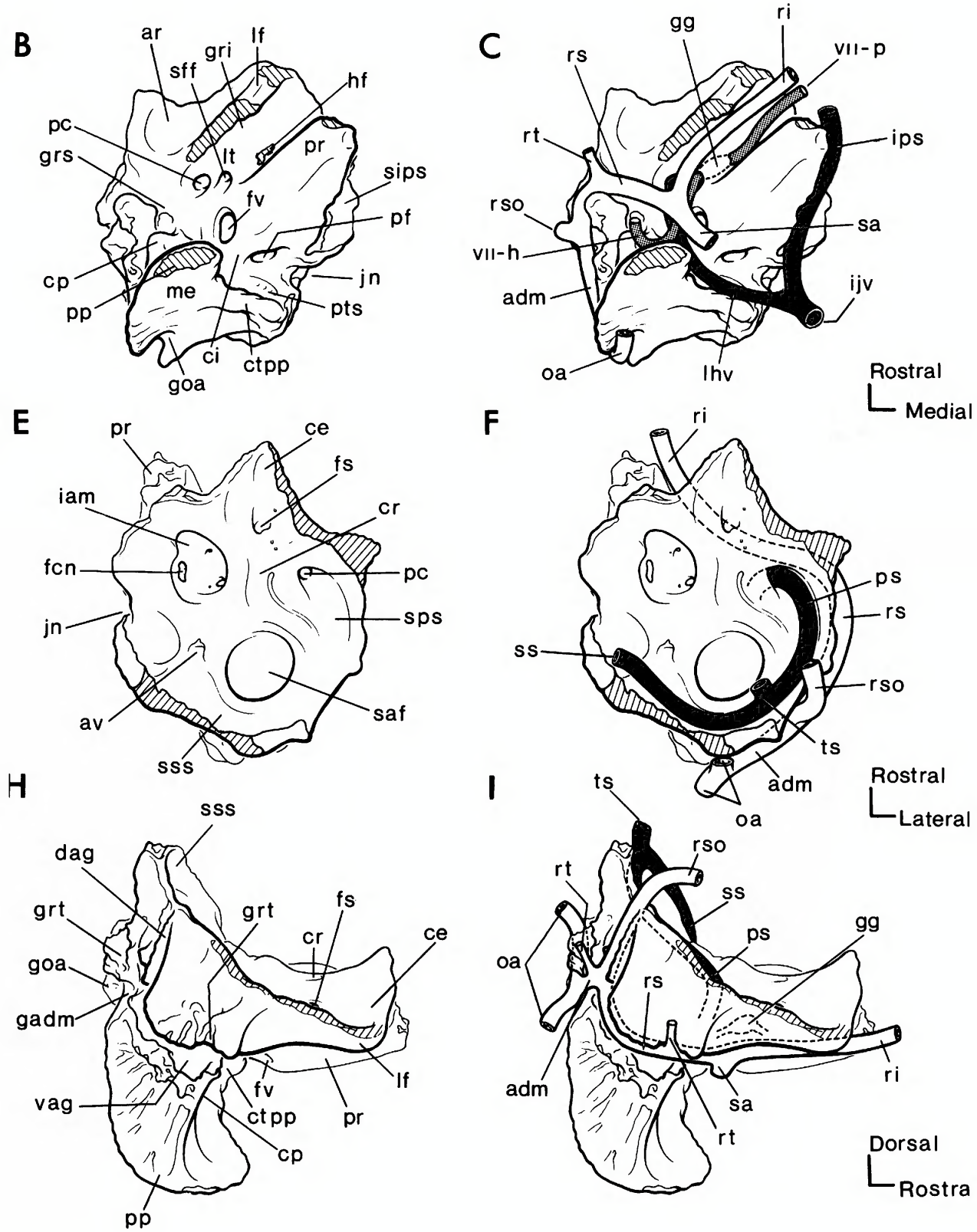


Fig. 1. Three views of the right petrosal from Khoobur, PSS-MAE-104. **A, B, C,** Ventral view. **D, E, F,** Dorsal view. **G, H, I,** Lateral view. Crosshatching indicates damaged surfaces. Facial nerve and vessels are reconstructed in C, F, and I (see text). Abbreviations: **adm,** arteria diploëtica magna; **ar,** anterolateral recess; **av,** aqueductus vestibuli; **ce,** cavum epiptericum; **ci,** crista interfenestralis; **cp,** crista parotica; **cr,** crista petrosa; **ctpp,** caudal tympanic process of petrosal; **dag,** dorsal ascending groove; **fcn,** foramen for cochlear nerve; **fs,** fenestra semilunaris; **fv,** fenestra vestibuli; **gadm,** groove for arteria diploëtica magna; **goa,** groove for occipital artery; **gri,** groove for ramus inferior; **grs,** groove for ramus superior; **grt,** groove for ramus temporalis; **hf,** hiatus Fallopii; **gg,** geniculate ganglion; **iam,** internal acoustic meatus; **ijv,** internal jugular vein; **ips,** inferior petrosal sinus; **jn,** jugular notch; **lf,** lateral flange; **lhv,** lateral head vein; **lt,** lateral trough; **me,** mastoid exposure; **oa,** occipital artery; **pc,** prootic canal; **pf,** perilymphatic foramen; **pp,** paroccipital process; **pr,** promontorium; **ps,** prootic sinus; **pts,** post-promontorial tympanic sinus; **ri,** ramus inferior; **rs,** ramus superior; **rso,** ramus supraorbitalis; **rt,** ramus temporalis; **sa,** stapedial artery; **saf,** subarcuate fossa; **sff,** secondary facial foramen; **sips,** sulcus for inferior petrosal sinus; **sps,** sulcus for prootic sinus; **ss,** sigmoid sinus; **sss,** sulcus for sigmoid sinus; **ts,** transverse sinus; **vag,** ventral ascending groove; **VII-h,** hyomandibular branch of facial nerve; **VII-p,** palatine branch of facial nerve.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small extent. Presumably, when complete, the lateral flange would have contributed to a partial floor below the lateral trough. The extent of this floor is uncertain, but it did not reach medially to the promontorium because contact scars are lacking. Lateral to the posterior margin of the lateral flange is a smooth, concave surface, which is broken anteriorly. The nature of this concavity, which we call the anterolateral recess, will be treated separately below. Posterior to this recess is a moderate eminence, which is continuous laterally with a low crest and medially with the broken base of the lateral flange. Immediately posterior to this region is a broad, transversely oriented sulcus. This sulcus continues onto the lateral surface of the petrosal and is interpreted as a ventral ascending groove for the ramus superior of the stapedial artery.

At the posterolateral corner of the petrosal is a stout, ventrally projecting paroccipital process (figs. 1G, H, 2). It is compressed lateromedially to form a crest whose long axis is oriented in the same direction as that of the promontorium. Two ridges extend from the paroccipital process: the crista parotica and the caudal tympanic process of the petrosal. The crista parotica runs anterodorsally and near its anterior end is a medially projecting broken prong of bone, which is identified as a tympanohyal, an ossified segment of Reichert's cartilage (fig. 2). The caudal tympanic process runs medially, almost reaching the jugular notch. Between the back of the promontorium and the paroccipital process, crista parotica, and caudal tympanic process of the petrosal is a recess, the postpromontorial tympanic sinus (figs. 1A, B, 2). In this recess anteromedial to the tympanohyal is an oval depression, the fossa for the stapedius muscle (fig. 2). Visible in ventral view along the entire lateral surface of the petrosal is an extensive articular surface, presumably for the squamosal (fig. 1A).

Dorsal View (fig. 1D, E, F)

This view shows three major structures: the internal acoustic meatus, subarcuate fossa, and cavum epiptericum (most of which is missing). The internal acoustic meatus lies in the anteromedial part of the petrosal. It is deep and contains three large foramina. The medial foramen, which is separated from the others by a low crista transversa, is oval and transmits the cochlear nerve. The anterolateral foramen, also oval, is the primary facial foramen through which the facial nerve leaves the cranial cavity to enter the cavum supracochleare. The circular posterolateral foramen is for the vestibular nerve.

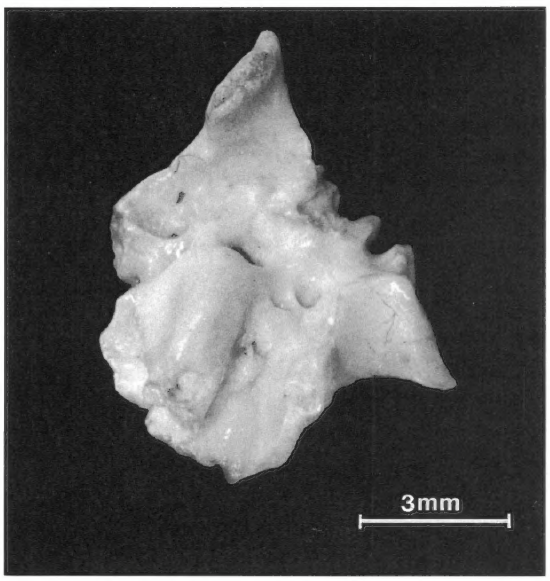
Posterolateral to the internal acoustic meatus is the deeply recessed subarcuate fossa, which in life housed the paraflocculus of the cerebellum. The gyrus of the anterior semicircular canal forms the posterior border of the subarcuate fossa. Between the subarcuate fossa and the internal acoustic meatus is a moderate-sized aperture for the endolymphatic duct, the aqueductus vestibuli.

Anterolateral to the subarcuate fossa is the cranial aperture of the prootic canal. Leading posteriorly from the aperture is a sulcus that bends medially posterior to and follows the outer contour of the subarcuate fossa. This sulcus cannot be traced beyond the level of the aqueductus vestibuli. In the prootic canal and in the sulcus running posteriorly from it, we reconstruct as the major occupant the prootic sinus, a distributary of the transverse sinus. In the part of the sulcus posterior and medial to the subarcuate fossa, we restore the sigmoid sinus, the other distributary of the transverse sinus. We believe that the major exit for the blood drained in the sigmoid sinus was the foramen magnum and not the jugular foramen, given the latter aperture's small size.

A shallow and incompletely preserved cavum epiptericum for the trigeminal (semilunar) ganglion lies lateral to and is separated by a thick crista petrosa from the internal acoustic meatus. The cavum is connected to the cavum supracochleare within the petrosal via a bony gap, the fenestra semilunaris, which also occurs in *Vincelestes* (Rougier et al., 1992) and some extant marsupials where it transmits no structures (Wible, 1990).

Lateral View (fig. 1G, H, I)

The lateral view is dominated by extensive articular surfaces for the squamosal and supraoccipital, both of which are largely complete. Also shown in this view are four well-



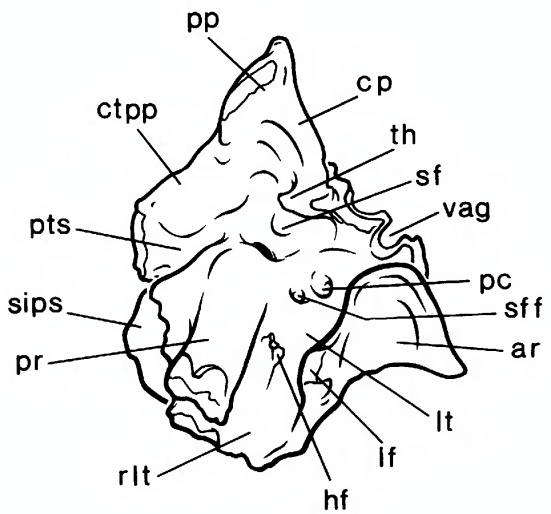


Fig. 2. Anteroventral views of the right petrosal from Khoobur, PSS-MAE-104. Cross-hatching indicates damaged surfaces. Abbreviations: **ar,** anterolateral recess; **cp,** crista parotica; **ctpp,** caudal tympanic process of petrosal; **hf,** hiatus Fallopii; **lf,** lateral flange; **lt,** lateral trough; **pc,** prootic canal; **pp,** paroccipital process; **pr,** promontorium; **pts,** post-promontorial tympanic sinus; **rlt,** recess of lateral trough; **sips,** sulcus for inferior petrosal sinus; **sf,** stapedius fossa; **th,** tympanohyal; **vag,** ventral ascending groove.

developed vascular grooves: from back to front, these are grooves for the occipital artery, arteria diploëtica magna, ramus supraorbitalis (dorsal ascending groove), and ramus superior (ventral ascending groove). There are also two smaller grooves for rami temporali, one continuous with the groove for the arteria diploëtica magna and the other with the ventral ascending groove. The grooves on the lateral surface of the petrosal, with the exception of that for the occipital artery, would have been enclosed in bony canals in life by the overlying squamosal.

Posterior View

The dominant feature in this view (not figured) is the broad mastoid exposure of the petrosal on the occiput (partially seen in fig. 1A, B, G, H). Along the dorsolateral edge of the mastoid exposure is a notch that contained the arteria diploëtica magna. Reconstructing the squamosal in place would create a composite posttemporal foramen and canal for the arteria diploëtica magna, as is the generalized condition in Eucynodontia.

Vascular Reconstruction (fig. 1C, F, I)

Selected soft tissues are restored in grooves, canals, and foramina on the Khoobur petrosal based on the anatomy of living mammals as discussed by Rougier et al. (1992) and Wible and Hopson (1995). Though not illustrated in the figures, most of the arteries were likely accompanied by small companion veins (Wible and Hopson, 1995).

The major components of the arterial pattern interpreted to be present in non-mammalian eucynodonts (Rougier et al., 1992) can be restored on the Khoobur petrosal. However, our arterial reconstruction differs from the primitive pattern in having an extremely short channel for the arteria diploëtica magna, a very long, horizontal, intramural ventral ascending channel for the ramus superior of the stapedial artery, and two narrow channels for temporal rami (fig. I). As in non-mammalian eucynodonts, there is no direct indication on the petrosal for the internal carotid and stapedial arteries. Nevertheless, given the distribution of both vessels among extant taxa, they were likely present

on the Khoobur petrosal. In living mammals, the internal carotid artery follows one of three alternative pathways, which may or may not be indicated by a sulcus on the petrosal: either transpromontorial, perbullar, or extrabullar (Wible, 1986). We do not reconstruct the internal carotid here, because there is no evidence supporting any one alternative. The large size of the sulci for the ramus superior and ramus inferior suggests the presence of the stapedial artery and, consequently, we reconstruct it.

The groove for the occipital artery in the Khoobur petrosal indicates that vessel was very large and probably the major contributor to the arteries on the sidewall of the braincase (fig. 1G, H, I). This was also probably the case in non-mammalian eucynodonts, given the relative sizes of their vascular channels (Rougier et al., 1992). This supposedly primitive pattern is altered in marsupials and placentals (except xenarthrans) by the reduction of the arteria diploëtica magna and the enlargement of either the external carotid or stapedial system (Wible, 1987). Among monotremes, the arteria diploëtica magna is large in the echidna (Kuhn, 1971), but is comparatively small in the platypus (Rougier et al., 1992; Wible and Hopson, 1995).

Several major veins can also be reconstructed on the Khoobur petrosal, including the sigmoid, prootic, and inferior petrosal sinuses and the lateral head vein. The most striking difference from the pattern thought to be primitive for non-mammalian eucynodonts (Rougier et al., 1992; Wible and Hopson, 1995) is the enclosure of the inferior petrosal sinus in a canal largely between the petrosal and basioccipital. The primitive course for this vessel is likely an endocranial one, as occurs in monotremes (Hochstetter, 1896) and is reconstructed for *Morganucodon* by Kermack et al. (1981).

DISCUSSION

Affinities of the Khoobur Petrosal

As stated above, a cladistic analysis of 44 characters across 15 ingroup taxa was performed to evaluate the affinities of the Khoobur petrosal. In the course of our character analysis, we encountered two problems in interpreting the morphology of the Khoobur petrosal: the position of the fossa incudis and the nature of the anterolateral recess (figs. 1A, B, 2). In most of the ingroup taxa studied here, there is a depression either lateral to or on the crista parotica for the dorsal process of the quadrate (the crus breve of the incus). In contrast, there is no fossa incudis on the petrosal of the outgroup taxa tritheledontids, tritylodontids, *Adelobasileus,* and *Sinoconodon.* The only surface on the Khoobur petrosal that resembles a fossa incudis is the anterolateral recess. However, this recess is too large and anteriorly placed to be a suitable candidate. Moreover, the bone underlying the recess is very thick, suggesting a mechanical robustness beyond that required to support the quadrate (incus). The only structure in this region that could require such a stout construction is the glenoid fossa or an area abutting the glenoid. *Vincelestes* has a similar thickened, laterally directed process on its petrosal that is continuous laterally with the glenoid fossa (Rougier, 1993). Therefore, we interpret the anterolateral recess of the Khoobur petrosal as either a part of the glenoid itself or, more likely, a bone providing support for it. We have seen a comparable arrangement in *Ornithorhynchus,* where the glenoid fossa continues rostrally onto the anterior lamina. However, in contrast to the condition in the Khoobur petrosal and *Vincelestes,* the anterior lamina in the platypus is not especially thickened near the glenoid and is not a conspicuous laterally directed process. Given our interpretation for the anterolateral recess, there is no suitable place for the fossa incudis on the Khoobur petrosal. The articular facet for the squamosal indicates that the squamosal bone contacted the lateral surface of the crista parotica. Consequently, we believe that the fossa incudis must have been on the squamosal lateral to the crista parotica, which as a primitive feature is peculiar in light of other, more advanced attributes of the Khoobur petrosal.

Appendix 2 shows the taxon-character matrix employed in our phylogenetic analysis. The branch and bound algorithm of PAUP and the **ie** command of Hennig86 identified nine equally most-parsimonious trees. The strict consensus tree is shown in figure 3. In an additional run on both programs, four

multistate characters (2, 9, 34, 41) for which hypotheses of transformation could be supported were coded as ordered, and the same nine trees were obtained.

As shown in the strict consensus tree, the Khoobur petrosal falls at a trichotomy with Triconodontidae and a clade comprising Theria and *Vincelestes,* the Prototribosphenida of Rougier (1993). In six of the nine trees obtained, the Khoobur petrosal forms a monophyletic group with Triconodontidae. This assemblage is supported by the presence of a deep recess in the anterior part of the lateral trough (character 26) and an intramural ventral ascending canal between the petrosal and squamosal (41). However, we are confident that the Khoobur petrosal does not belong to the family Triconodontidae because of the striking differences, including, for example, the anterolateral recess and caudal tympanic process in the Khoobur specimen. Yet it may belong to a triconodont or to its sister group as we use the term here (see Materials and Methods). In the remaining three trees, the Khoobur petrosal is linked to the prototribosphenidan clade by a caudal tympanic process of the petrosal (12), a postpromontorial tympanic sinus (13), a thickened laterally directed surface of the petrosal related to the glenoid fossa (32), and two reversals, i.e., presence of crista parotica–squamosal contact (17) and absence of crests demarcating a tensor tympani fossa (27). Although more characters support linkage of the Khoobur petrosal with the prototribosphenidan clade than with Triconodontidae, both hypotheses are equally parsimonious considering the tree as a whole.

Regarding the affinities of the Khoobur petrosal, the results of our computer analysis are not conclusive. Considering the fossil record from Khoobur, a preliminary faunal list was published by Clemens et al. (1979), compiled from Russian bibliographies, mainly those of Beliajeva et al. (1974) and Dashzeveg (1975). Additional taeniolabidoid multituberculate material was described by Trofimov (1980) and Kielan-Jaworowska et al. (1987); amphidontid symmetrodonts by Trofimov (1980); cladotherians by Dashzeveg (1979, 1994); and tribosphenidans by Dashzeveg and Kielan-Jaworowska (1984), Kielan-Jaworowska and Dashzeveg (1989), and Sigogneau-Russell et al. (1992). The material described to date consists of isolated teeth and upper and lower jaws. An additional taxon, *Prodelttheridium kalandadzei* [sic] Trofimov (1984) cited in Reshetov and Trofimov (1984), was said to be from Khoobur. However, it was never figured or described and, consequently, was considered to be nomen nudum by Kielan-Jaworowska and Nessov (1990).

To associate the isolated petrosal with a taxon known from dentition and given the possible relationships suggested by our analysis, we used nearly complete skulls and lower jaws of a Cloverly triconodontid (MCZ 19974) and *Vincelestes* (Rougier, 1993) to predict skull length for the Khoobur petrosal. The estimated skull length was about 4.0 cm based on the triconodontid and 3.5 cm based on *Vincelestes.* There are two taxa reported thus far from Khoobur with predicted skull lengths (based on lower jaw length) approximating that calculated for the Khoobur petrosal: the gobiconodontid *Gobiconodon borissiaki* (Trofimov, 1978) at about 5.0 cm and the symmetrodont *Gobiodon infinitus* (Trofimov, 1980) at between 4.1 and 4.6 cm. If gobiconodontids form a monophyletic group with triconodontids, as tentatively suggested by Rowe (1993), either assignment is possible: triconodontid affinities on the one hand (with *Gobiconodon borissiaki*) and prototribosphenidan affinities on the other (with *Gobiodon infinitus*).

Gobiconodon is also known from the Cloverly Formation of North America (Jenkins and Schaff, 1988). A separate species, *G. ostromi,* was recognized for these specimens, with a skull length estimated to be more than 10.0 cm by Jenkins and Schaff (1988). Among other cranial material, an isolated left squamosal was recovered. This squamosal preserves a nearly complete glenoid fossa that is separated from the squama by a distinct neck. The presence of a neck would preclude any contact between the glenoid fossa and the petrosal, which we have interpreted above to be present in the Khoobur petrosal, given the morphology of the anterolateral recess. If the Khoobur petrosal is affiliated with Mongolian triconodonts, either *Gobiconodon* from the Gobi and *Gobiconodon* from North America are not closely related or the glenoid

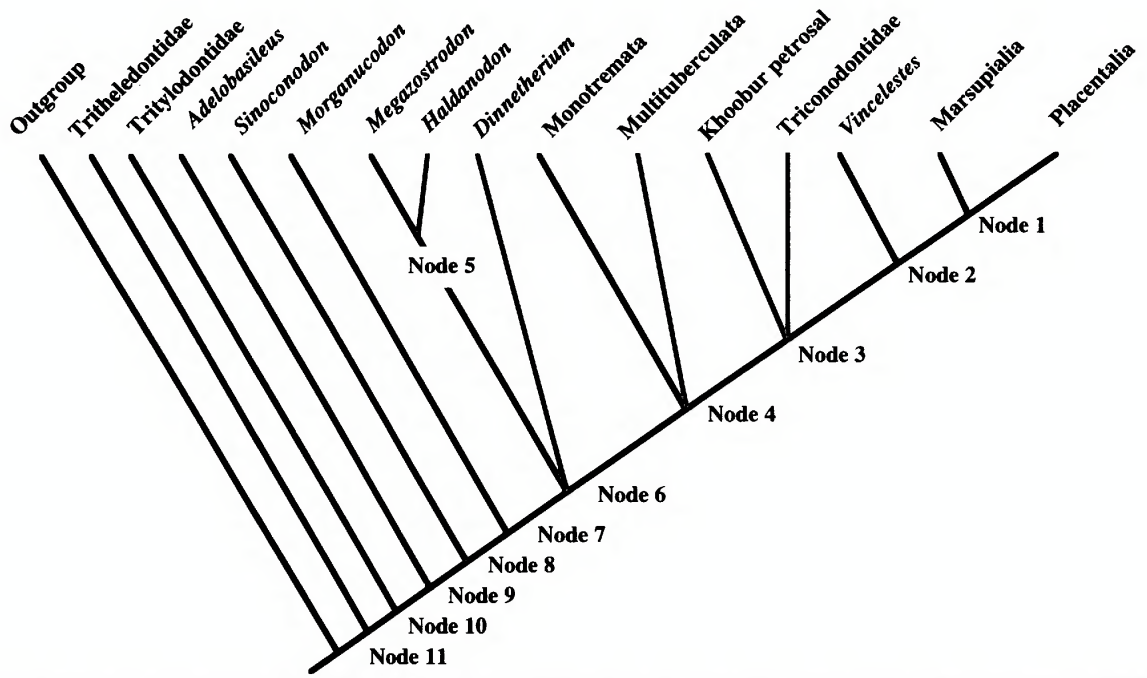


Fig. 3. Strict consensus tree of nine equally most parsimonious trees produced by PAUP and Hennig86. The strict consensus (nelsen) on Hennig86 has the following parameters: branch length = 90; consistency index = 0.58; and retention index = 0.73; these values on the nine individual trees in Hennig86 are 85, 0.62, and 0.77, respectively.

of *Gobiconodon* varies remarkably at the species level (i.e., continuity with the petrosal on the one hand versus separation via a distinct neck on the other). Given that the lower jaws and dentitions of the North American and Mongolian forms are remarkably similar, we agree with Jenkins and Schaff (1988) that they belong to the same genus. Furthermore, we would not expect such an extreme difference in glenoid morphology between two species of the same genus. Consequently, we think it unlikely that the Khoobur petrosal belongs to *Gobiconodon* sp. We conclude that it belongs to either an as yet unknown triconodont or to a primitive holotherian, which in the context of the currently known Khoobur fauna would be the symmetrodont *Gobiodon infinitus*. Holotheria (Hopson, 1994) includes the common ancestor of *Kuehneotherium* and therians plus all its descendants.

Implications for Mammaliamorph Phylogeny

Recently, there have been a number of studies that have discussed the affinities of some of the taxa included here and have employed some petrosal characters: Rowe (1988, 1993), Wible (1991), Lillegraven and Krusat (1991), Crompton and Luo (1993), Wible and Hopson (1993), Lucas and Luo (1993), and Luo (1994). Our analysis includes all Mesozoic mammaliamorphs for which the petrosal is currently known. Comparisons of our results with those of the authors mentioned above highlight the following problematic issues in mammaliamorph phylogeny.

1) Tritheledontidae and Tritylodontidae Relationships. There is currently debate as to whether tritheledontids or tritylodontids are more closely related to mammaliaforms. Our analysis does not provide a rigorous test of this problem, which requires that more nonmammalian cynodonts be considered as ingroup taxa. Nevertheless, our analysis of petrosal characters supports tritylodontids in that position, in agreement with Rowe (1988, 1993), Wible (1991), Wible and Hopson (1993), Lucas and Luo (1993: fig. 14b), and Luo (1994: fig. 6.8). Two unequivocal and three equivocal synapomorphies support this relationship (appendix 3, node 10). Other

analyses using some petrosal characters together with characters from other systems reach the reverse conclusion (Lucas and Luo, 1993: fig. 14a; Luo, 1994; Luo and Crompton, 1994). Given these conflicting results, it appears that this phylogenetic problem cannot be resolved with currently available information. Of crucial importance is a better understanding of the cranial and postcranial skeleton of tritheledontids.

2) Basal Mammaliaform Relationships. As defined by Rowe (1988), Mammaliaformes comprises the common ancestor of *Morganucodon* and Mammalia plus all its descendants. In our analysis of petrosal characters, *Sinoconodon* and *Adelobasileus* are the successive sister taxa to Mammaliaformes. In their description of *Adelobasileus,* Lucas and Luo (1993: fig. 14) presented two phylogenetic hypotheses: a strict consensus tree, which includes *Adelobasileus* within Mammaliaformes and *Sinoconodon* as the first outgroup, and their preferred tree, which places *Adelobasileus* and *Sinoconodon* at a trichotomy with other mammaliaforms. Criteria for their preference of trees are not specified. Whereas their strict consensus tree contradicts ours, their preferred tree does not. If our hypothesis is correct, there is congruence between the branching pattern and age of the taxa, because *Adelobasileus* is known from the Carnian and the others from the Liassic. The basal position of *Adelobasileus* is supported here by two unequivocal and three equivocal synapomorphies (appendix 3, node 9).

3) *Haldanodon* Relationships. The only basicranial material known for docodonts is the Oxfordian or Kimmeridgian *Haldanodon exspectatus* described by Krusat (1980) and Lillegraven and Krusat (1991). In the latter paper, 149 craniomandibular characters were scored among four ingroup taxa: *Haldanodon, Sinoconodon, Morganucodon,* and a collective group called other mammals. The resulting phylogenetic hypothesis places *Haldanodon* as the outgroup to the other ingroup taxa. This contrasts with the more widespread view that docodonts are mammaliaforms—that is, related to morganucodontids or even more derived (Crompton and Jenkins, 1979; Crompton and Sun, 1985; McKenna, 1987). To obtain Lillegraven and Krusat's (1991) position for *Haldanodon,* it is necessary to add four steps to the shortest trees of our study. A monophyletic grouping of *Haldanodon* and *Megazostrodon* is weakly supported here by two unequivocal synapomorphies, one of which is a reversal, plus one equivocal trait (appendix 3, node 5). Similarly, Butler (1988) suggested a closer relationship of docodonts to *Megazostrodon* than to *Morganucodon.*

4) Interrelationships of Mammals. Mammalia, as defined by Rowe (1988), comprises the latest common ancestor of monotremes, marsupials, and placentals plus all its descendants. In our analysis, Mammalia is supported by four unequivocal and two equivocal synapomorphies (see appendix 3, node 4). As follows from Rowe's definition, the scope of Mammalia is dependent on the position of monotremes among Mesozoic taxa, which is a controversial topic in recent literature. Prior to the discovery of the Early Cretaceous monotreme *Steropodon galmani* (Archer et al., 1985), there was a general consensus that monotremes were "non-therian mammals" (Kermack, 1967; Hopson, 1970; Kielan-Jaworowska, 1970; Crompton and Jenkins, 1979). However, after that discovery, monotremes were allied with different groups of holotherians: tribosphenidans (Archer et al., 1985), peramurids (Kielan-Jaworowska et al., 1987; Jenkins, 1990), dryolestoids (Bonaparte, 1990; Archer et al., 1993), and symmetrodonts (Hopson, 1994). Our analysis does not support holotherian affinities for monotremes (see also Rougier, 1993), unless multituberculates and triconodonts are also considered to be holotherians. We see no compelling evidence for including multituberculates and triconodonts within Holotheria, because they do not share the reversed-triangles molar pattern used to diagnose that grouping. The same conclusion is implicit in the cladograms published in Rowe (1988, 1993) and Wible and Hopson (1993), but these authors did not explicitly address the problem of the hypothesis of holotherian affinities for monotremes. Removal of monotremes from Holotheria has important implications for predicting the biology of basal holotherians (e.g., reproduction, thermoregulation) as attempted by Jenkins (1990).

Another controversial topic in recent literature is the phylogenetic position of mul-

tituberculates. As was the case for monotremes, multituberculates have been traditionally allied with "non-therian mammals," and several recent authors (e.g., McKenna, 1987; Lillegraven and Krusat, 1991; Kielan-Jaworowska, 1992) have considered multituberculates as an ancient lineage possibly outside mammaliaforms. In contrast, Kemp (1983, 1988) tentatively grouped multituberculates with cladotherians, and Rowe (1988) and Wible (1991) placed multituberculates at an unspecified rank among holotherians. In our analysis of petrosal characters, three of the nine trees as well as reweighting of the data set support a monophyletic grouping of multituberculates and monotremes (see also Wible and Hopson, 1993); in the remaining six trees, multituberculates are more closely related to triconodontids, the Khoobur petrosal, and prototribosphenidans than to monotremes.

Triconodontids, also traditionally considered "non-therians," are linked in our analysis to the Khoobur petrosal and prototribosphenidans by two unequivocal and six equivocal synapomorphies (appendix 3, node 3). Following Rowe (1993), we apply the term Theriimorpha for this grouping, but our analysis renders it a less inclusive category because multituberculates are excluded. No other analyses have postulated such affinities for triconodontids. Several complete skulls from the Cloverly Formation have been partially described (Crompton and Jenkins, 1979; Crompton and Sun, 1985; Crompton and Luo, 1993), and their full description will greatly increase the database for resolving the affinities of this group.

CONCLUSIONS

Our phylogenetic analysis of the Khoobur petrosal restricts its affiliation to two possible groups: either with triconodontids or with holotherians. In the fauna, the triconodont *Gobiconodon borissiaki* and the symmetrodont *Gobiodon infinitus* match the predicted size. However, complementary morphological information from *Gobiconodon ostromi* makes the assignment of the petrosal to *G. borissiaki* questionable. We conclude that the Khoobur petrosal is either that of an as yet unknown triconodont or a holotherian, which is in the size range of *Gobiodon infinitus*.

Given the nature of the Khoobur fossil described here, we were compelled to restrict our analysis to characters of the petrosal bone and associated structures. Wible and Hopson (1993) presented an analysis that was similar in scope, both morphologically and taxonomically. Subsequent to their publication, new relevant taxa and additional information from previously known forms became available. The inclusion of these data in our analysis resulted in trees with topologies different from those in Wible and Hopson (1993). We attribute these differences to an increase in the number of taxa studied from 11 to 15, an increase in the number of characters (30 to 44 from the petrosal), and fewer missing data. In spite of a more complete data set, we obtained poorer resolution than did Wible and Hopson (1993). Some nonconflicting characters used by those authors were rendered homoplastic in our analysis with the increased number of taxa studied and the decreased amount of missing data.

The topological changes resulting from the addition of a few taxa and characters are significant. Our results highlight the impact on phylogeny of a dramatically increasing morphological database for Mesozoic mammaliamorphs.

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APPENDIX 1

Petrosal Characters

1. Sutural relation of prootic and opisthotic – unfused (0) or fused to form petrosal (1).
2. Petrosal promontorium – absent (0), incipient but distinctive with anterior part covered by basisphenoid wing (1), or inflated without basisphenoid wing (2).
3. Promontorium shape – triangular in outline, wider posteriorly (0) or fingerlike outline (1).
4. Ventral crest on promontorium – absent (0) or present (1).
5. Fenestra vestibuli margin – with thickened osseous ring (0) or smooth, without osseous ring (1).
6. Fenestra vestibuli shape – round, stapedial ratio less than 1.5 (0) or elongate, stapedial ratio greater than 1.5 (1).
7. Wall separating perilymphatic foramen from jugular foramen – absent (0) or present (1).
8. Channel for perilymphatic duct – open (0) or enclosed in osseous canal, a cochlear aqueduct (1).
9. Cochlear duct – straight (0), bent (1), or coiled, 360° (2).
10. Secondary spiral lamina – absent (0) or present (1).
11. Semicircular canals – enclosed by opisthotic, supraoccipital, and exoccipital (0) or enclosed by opisthotic (petrosal) (1).
12. Caudal tympanic process of petrosal – absent (0) or present (1).
13. Post-promontorial tympanic sinus – absent (0) or present (1).
14. Fossa for stapedius muscle – absent (0) or present (1).
15. Paroccipital process with distinct, ventrally directed projection for muscle attachment – absent (0) or present (1).
16. Tympanohyal – separate (0) or attached to petrosal (1).
17. Crista parotica-squamosal contact – present (0) or absent (1).
18. Quadrate (incus) articulation in fossa incudis on petrosal – absent (0) or present (1).
19. Pterygoparoccipital foramen position relative to fenestra vestibuli – at same level or posterior to (0) or anterior to (1).
20. Prootic canal – absent (0), present within petrosal (1), or present between petrosal and squamosal (2).
21. Cranial aperture of prootic canal – in rear of cavum epiptericum (0) or at anterodorsal margin of subarcuate fossa (1).
22. Tympanic aperture of prootic canal – separate from (0) or confluent with pterygoparoccipital foramen (1).
23. Cavum epiptericum floor – open ventrally (0), partially floored by petrosal (1), floored, primarily by petrosal (2), or floored, primarily by alisphenoid (3).
24. Facial ganglion floor – open ventrally (0) or floored by petrosal (1).
25. Lateral trough of petrosal – absent (0) or present (1).
26. Deep recess in anterior part of lateral trough – absent (0) or present (1).
27. Crests demarcating distinct fossa for tensor tympani on petrosal – absent (0) or present (1).
28. Craniomandibular joint position relative to fenestra vestibuli – level with (0) or anterior to (1).
29. Petrosal (prootic) contact with quadrate ramus of alisphenoid (epipterygoid) – elongate (0) or greatly reduced or absent (1).
30. Lateral flange of petrosal (prootic) – laterally directed shelf (0), ventrally directed crest (1), or absent (2).
31. Vascular foramen in lateral flange of petrosal (prootic) – absent (0) or present (1).
32. Thick, laterally directed surface of petrosal related to glenoid fossa – absent (0) or present (1).
33. Sulcus along basioccipital surface of petrosal (for inferior petrosal sinus) – absent (0) or present (1).
34. Cavum supracochleare – absent (0), present, with incomplete wall separating it from cavum epiptericum (fenestra semilunaris present) (1), or present, completely enclosed by bone (2).
35. Separate foramina for cochlear and vestibular nerves – absent (0) or present (1).
36. Common depression housing foramina for facial and vestibulocochlear nerves – absent (0) or present (1).
37. Pila antotica – ossified base present (0) or absent (1).
38. Anterior lamina of petrosal (prootic) – present (0) or greatly reduced or absent (1).

39. Contribution of anterior lamina of petrosal (prootic) to cranial wall – extends forward to posterior border of exits for mandibular and maxillary nerves (0), expanded forward anterior and dorsal to nerve exits, no contact with orbitosphenoid (1), or expanded forward and contacting orbitosphenoid (2).
40. Number of exits for mandibular and maxillary nerves – single (0) or multiple (1).
41. Ventral ascending groove or canal – open laterally (0), intramural, within petrosal (1), or intramural, between petrosal and squamosal (2).
42. Orientation of ventral ascending groove or canal – vertical (0) or horizontal (1).
43. Dorsal ascending groove or canal – open laterally (0) or intramural or endocranial (1).
44. Posterior opening of posttemporal canal – separated from margin of occiput by tabular (0) or positioned close to margin of occiput, bordered dorsolaterally by squamosal (1).

Most of the above characters are taken directly or are modified from the following references, to which the reader is referred for additional information.

Characters:

1, 7, 9, 16, 28, 35, 37 – Rowe (1988)
2, 4, 5, 44 – Lucas and Luo (1993)
6, 12, 13 – Wible (1990)
8, 38 – Kermack et al. (1981)
11 – Luo et al. (1995)
25, 33, 40 – Lillegraven and Krusat (1991)
14, 15, 20, 21, 22, 23, 27, 34, 36, 39, 41, 43 – Wible and Hopson (1993)
24 – Crompton and Sun (1985)
29, 31 – Wible (1991)
30 – Luo (1994)

APPENDIX 2
Taxon-Character Matrix

Taxon	Character*								
	5	10	15	20	25	30	35	40	44
Outgroup	00NN0	00000	00000	0000?	??000	N0000	?0000	?0000	0000
Tritheledontidae	?0NN0	0100?	00000	00000	NN000	N0000	00001	00000	0000
Tritylodontidae	10NN0	0100?	00010	11000	NN000	N0000	10001	10001	0010
Adelobasileus	11001	0100?	?0000	?0001	?0101	000?1	1000?	?0011	0011
Sinoconodon	12011	0100?	10011	00001	00111	00000	10001	?0011	0011
Morganucodon	12001	01000	10011	01101	10111	00001	10001	00011	0011
Megazostrodon	12011	0100?	10011	?1101	101?1	00001	100?1	??010	00?1
Haldanodon	12011	01000	10011	1?111	10?11	00001	10001	11010	00??
Dinnetherium	12001	0100?	10011	11101	10111	?1001	100?1	??0??	00?1
Triconodontidae	12101	11000	10011	11111	10211	11101	00021	1?011	2111
Multituberculata	12101	01000	10011	11111	11211	01011	00101	10021	1111
Vincelestes	12001	11111	11111	11111	10211	00111	11011	11011	1111
Monotremata	12001	01010	10001	11101	11211	00011	00001	10021	1011
Marsupialia	12001	01121	11110	101N2	1N310	N0112	00121	111N1	NNN1
Placentalia	12001	11121	11110	10110	NN310	N0112	00121	111N1	NN11
Khoobur Petrosal	12101	11000	11111	10011	10211	10111	01111	1?0??	211?

* ? = missing data or multistate condition for outgroup; N = not applicable; 0–3 = character states (see appendix 1).

APPENDIX 3

Diagnoses of Nodes

Nodes are diagnosed by listing the derived conditions for characters in appendix 1. Multistate characters or reversals are depicted within parentheses ( ) following the character number. Asterisks (*) denote equivocal characters. These are listed at the less inclusive node, and the more inclusive distribution is indicated within brackets [ ].

Node 1 – Theria
- 15(0) – paroccipital process absent
- 17(0) – crista parotica/squamosal contact present
- 23(3) – cavum epiptericum with alisphenoid floor
- 25(0) – lateral trough absent
- 30(2) – lateral flange absent
- 33 – inferior petrosal sulcus present
- 38 – anterior lamina greatly reduced or absent
- 9(2)* – cochlear duct coiled [node 2]
- 34(2)* – cavum supracochleare enclosed [node 3]

Node 2 – Prototribosphenida
- 8 – cochlear aqueduct present
- 10 – secondary spiral lamina present
- 12* – caudal tympanic process of petrosal present [node 3]
- 13* – post-promontorial sinus present [node 3]
- 37* – pila antotica absent [node 3, 5]

Node 3 – Theriimorpha
- 6 – fenestra vestibuli elongated
- 28 – craniomandibular joint anterior to fenestra vestibuli
- 19* – pterygoparoccipital foramen anterior to fenestra vestibuli [node 4]
- 42* – ventral ascending groove or canal horizontal [node 4]

Node 4 – Mammalia
- 23(2) – cavum epiptericum with petrosal floor
- 29 – quadrate ramus of alisphenoid absent
- 31(0) – lateral flange vascular foramen absent
- 41(1) – ventral ascending groove or canal intramural in petrosal

Node 5 – *Megazostrodon* + *Haldanodon*
- 4 – ventral crest on promontorium
- 40(0) – single exit for mandibular and maxillary nerves

Node 6
- 16 – tympanohyal on cranium
- 36* – facial and vestibulocochear nerves in common depression [node 10]

Node 7 – Mammaliaformes
- 17 – crista parotica/squamosal contact absent
- 18 – fossa incudis present on petrosal
- 21 – cranial aperture of prootic canal near subarcuate fossa
- 30(1)* – lateral flange ventrally directed [node 9]

Node 8
- 15 – paroccipital process with ventral projection
- 24 – facial ganglion floored by petrosal
- 2(2)* – promontorium inflated without basisphenoid wing [node 9]
- 11* – semicircular canals enclosed by petrosal [node 9]
- 14* – stapedius fossa present [node 10]

Node 9
- 5 – margin of fenestra vestibuli without ring
- 20(1) – prootic canal present in petrosal
- 23(1) – cavum epiptericum with partial petrosal floor
- 25 – lateral trough present
- 39(1) – anterior lamina expanded dorsal to mandibular and maxillary nerve exits
- 44 – posttemporal canal with squamosal border

Node 10 – Mammaliamorpha
- 31 – lateral flange vascular foramen present
- 40 – multiple foramina for mandibular and maxillary nerves
- 1* – prootic and opisthotic fused [node 11]

Node 11
- 7 – distinct jugular and perilymphatic foramina
- 35 – cochlear and vestibular nerves in separate foramina
- 43 – dorsal ascending groove or canal intramural or endocranial

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